RECENT UNUSUAL UK COLLEMBOLA RECORDS – ENTOMOBRYOMORPHA AND PODUROMORPHA

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ABSTRACT

Substantial updates to our understanding of the distribution of nine species of UK Collembola (Suborders: Entomobryomorpha and Poduromorpha) are reported. We note four species omitted from the main UK key (one very common) and we note the rediscovery of five species in the UK after >50 years. Three of these were previously only collected in the UK by Richard Bagnall in the 1930s.

Key Words: *Axelsonia littoralis, Desoria trispinata, Entomobrya intermedia, Folsomia inoculata, Folsomides angularis, Friesea acuminata, Heteromurus major, Megaphorura, Mesogastrura libyaca, Mesentotoma dollfusi.*

INTRODUCTION

Collembola (springtails) are among the commonest land animals in the UK, occurring at densities upwards of 10,000 animals m^{-2} (Hopkin, 2007), but they are frequently overlooked due to small size, cryptic habits and lack of economic impacts. There has been a National Collembola Recording Scheme in the UK since 2005, initiated by Steve Hopkin. It is maintained now by the author, having about 15000 records from 317 species, historically expanding by around 350 records per year. (This will have to accelerate to keep pace with the volume of records coming from county recorders directly to the NBN). A few of these have been subjected to 'barcoding' (Shaw & Benefer, 2015). Unsurprisingly the majority of these are of common species, but interspersed with more unusual records. These include new, invasive species, and those which appear to be native but scarce (or overlooked). The aim of this note is to highlight a selection of recent records of Collembola that are either genuinely rare, or apparently so due to their being omitted from the Field Studies Council AIDGAP key (Hopkin, 2007). This review will be confined to the groups containing the larger species – the Entomobryomorpha and Poduromorpha. (The other main group, the Symphypleona, contains several invasive but undescribed species in the UK, and will form the basis of a subsequent article).

RESULTS

Terrestrial species

Entomobryomorpha

Entomobrya intermedia Brook

This is undoubtedly the commonest of the UK's under-recorded Collembola, since it is in fact one of our commonest and most widespread species. However, in Hopkin (2007) and Fjellberg (2007) this species keys out as *Entomobrya nivalis* L., though with an imperfect fit. Hopkin (2007) considered *E. intermedia* to be a synomym of *E. nivalis* L., implicitly assuming that the small variations in colour patterns on abd(omen)4 were intra-specific variation. The difference lies in the purple/brown patterning on this segment, which takes two different forms: a 'U' shape above two

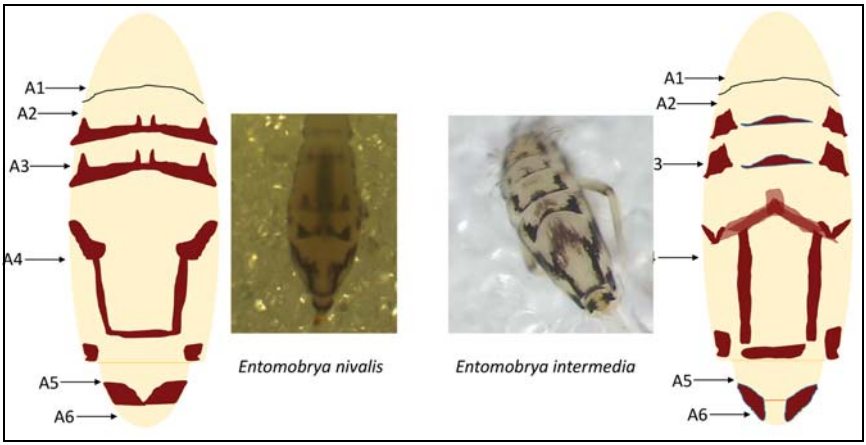

Fig. 1. The dorsal pigmentation of *Entomobrya intermedia* compared to *Entomobrya nivalis*.

dots, or a 'house' shape above three dots (Fig. 1). Jordana (2012) identifies *E. intermedia* as a distinct species, endemic to the UK (hence its non-inclusion in Nordic keys). These two species can occur together, but generally do not. Barcoding of *Entomobrya* specimens from around Great Britain showed that the two colour patterns form distinct lineages without overlap, so in fact are valid species (Faria, 2015; Faria, Emerson & Shaw, under review). The difference in COI sequences between the lineages suggested a separation in excess of 40,000 years, predating the last glacial maximum. It is not clear whether our three pre-war records of *E. intermedia* are in fact this species rather than *E. nivalis*. The diagram of *Deegeria annulata* (Lubbock) = *E. nivalis* in Lubbock (1873) shows the colour pattern of *E. nivalis* accurately.

Setting aside pre-war records, *Entomobrya intermedia* was first formally recorded in the UK in 2003 (in the author's garden near Dorking), though it was certainly there earlier. The photo of *E. nivalis* in plate 12A of Hopkin (2007) in fact shows the colour pattern of *E. intermedia*, suggesting an alternative claim for the first record of this species was in Steve Hopkin's garden near Reading. So far all records for this species have been in England and Wales, except for a single record from Fife (Fig. 2). The Collembola of Dundreggan and StrathFarrar (north of Loch Ness) have been the subject of a determined sampling campaign spread over two years collecting material from a variety of habitats (Shaw & Featherstone-Watson, in prep.). This found no *E. intermedia*, though many *E. nivalis*, agreeing with a southerly distribution for *E. intermedia*. During the 2012 sampling campaign to collect *Entomobrya* from around the UK (Faria, 2015), 75 localities produced either *E. nivalis* or *E. intermedia*. In this UK-wide dataset there was a negative correlation between the counts of *E. intermedia* and those of *E. nivalis* ($r_s = -0.38$, $df = 73$, $p < 0.01$), again suggesting a degree of inter-specific niche separation between these two congeners.

Entomobrya sp nov

We have three records of a species of *Entomobrya* whose eye-catching and distinctive colour pattern (Fig. 3) does not match any known species (Jordana, 2012,

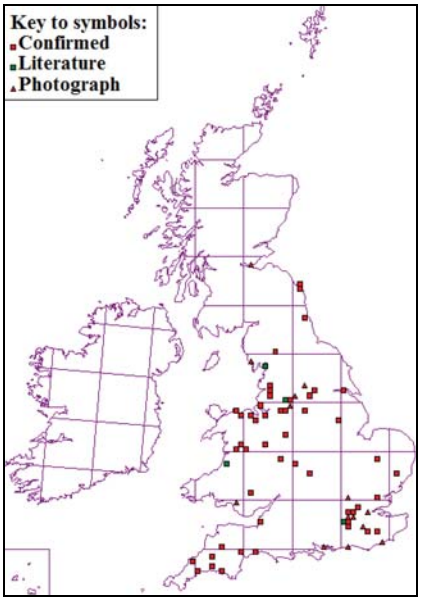

Fig. 2. The UK distribution of *Entomobrya intermedia*.

Fig. 3. *Entomobrya* sp (cf. *E. imitabilis*). Photo by John Byrne, January 2017.

pers. comm.). Its closest approximation is *Entomobrya imitabilis* Stach, a species described solely from one specimen collected in China. This is presumably a non-native invasive, though its distribution is unusual; one record each from north Wales, south Wales and Jersey.

Records: Llangollen (North Wales, SJ21290-42097) photo15.i.2015 by Keith Evans; Pembroke (South Wales SN 08098 05081) photo 02.iv.2017 by J. Byrne; St Ouen Jersey, photo 02.iv.2018 by S. Robson.

Folsomides angularis (Axelson)

This tiny white isotomid, made distinctive by its five black ocelli (Fig. 4), has only been recorded once before in the UK, by Bagnall from Whitley Bay in 1928 (as *Proisotoma angularis*). No specimens survive from this collection and Hopkin regarded its status as unclear. About 15 animals of this species were collected by PJAS from a bed of an inert granular industrial waste ('Lytag') at Tilbury power station in Essex. The Lytag had been abandoned for over 20 years, and was colonised with *Sedum anglicum* and *Cladonia* lichens. *Folsomides angularis* were collected from one sample by Tullgren extraction of the top 5 cm. A second (single) specimen was extracted from a 25 year old pulverised fuel ash experimental plot nearby (Shaw, 2012). These industrial waste habitats are soilless, free draining and very dry, as is typical for *Folsomides* species (Shaw & Buckhoree, 2000; Hopkin, 2007). These were easily overlooked among the much larger and more frequent specimens of *Entomobrya multifasciata* (Tullberg), *Parisotoma notabilis* (Bagnall) and *Cryptopygus thermophilus*(Axelson).

Records: Whitley Bay, Northumberland NZ3573 August 1928 col. R Bagnall; Lytag at Tilbury power station, Essex TQ65617648 col 03.x.2017 col PS; PFA deposits at Tilbury Power station, Essex TQ65707610 on 03.x.2017 col PS.

Heteromurus major (Moniez)

This springtail is probably widespread in the south of the UK, but is massively

Fig. 4. *Folsomides angularis*, Tilbury Power Station, 3 Oct 2017.

overlooked since it is absent from all the available UK keys to the group and easily mis-identified as a *Lepidocyrtus* species. It is a brown springtail with abundant oval scales on its body and 8 + 8 occelli (Fig. 5). This combination along with a large abdominal segment 4 closely resembles *Lepidocyrtus*. The key difference is that the midline ratio of abd4/ad3 is slightly below 2.0 (typically 1.9), while in all *Lepidocyrtus* this ratio is closer to 2.5. The key step in Hopkin (2006) uses a ratio of 2.0 as the separator between the "large abdomen IV genera" (*Lepidocyrtus*, *Entomobrya*, *Seira* and others) and other Collembola, so a ratio of 1.9 is easy to mis-judge. Also the antennae differ, with the terminal segment in *Heteromurus* being annulated, though the antennae are prone to damage both during life and

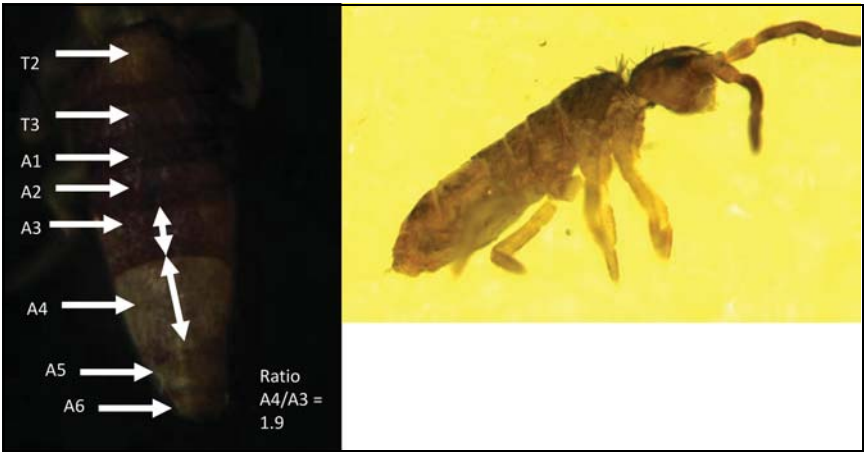

Fig. 5. *Heteromurus major*.

post-mortem. International collections of this species show an unusually high genetic diversity (Lucik *et al*., 2018), and correspondingly the colour in UK collections of this species is not constant, varying from dark brown to a paler pinky brown (especially on abdomen 4). It has a strongly southern distribution in Britain (Fig. 6), and has been found in a variety of habitats, primarily open and anthropogenic (gardens, industrial sites), but also leaf litter in ancient woodland (Boookham Common), and in the littoral fringe by Chesil beach. The earliest record in the UK is 2000 (from weed-suppressing mulch at RHS Wisley Garden collected by the author 04.x.2000), but it was surely widely present and overlooked previously. Mari Mutt (1980) reviews this species (as part of a review of the genus) and noted it occurring in mainland Europe but not in the UK.

Records: RHS Wisley flower bed TQ06177 58483, col. PS on 04.x.2000; Isabella Plantation, Richmond Park TQ200717, photo by Toby Barton 27.iv.2008; RHS Wisley TQ06330 59316, col. S. al Beidh 08.iv.2010; East Malling, Kent TQ5770 col by M. Fountain 2011; Bookham Common TQ13416 56836: col by PS on 09.vii.2012; RHS Wisley (Howards Field), TQ06235 59222 col. S. Bird, multiple records July 2011–April 2013;

RHS Wisley (Deers farm) TQ06330 59316, col. S. Bird, multiple records July 2011–April 2013; Market Drayton SJ64701 32856, col. C. Bell 01.v.2016; Fleet, Dorset, SY67133 74762 col by ST 01.v.2017; garden near Exeter, Devon SX 95252 93726, col. M. Shepherd 05.vii.2018.

Desoria trispinata (MacGillivray)

This is probably a synanthropic species (Fig. 7), originally recorded from Ohio, USA that is a planetary globe-hopper. It is likely to be widespread but badly under-recorded in the UK, since it is absent from Hopkin (2007). It is easily mis-identified for the (very common) *Parisotoma notabilis* Schäfer (but has eight eyes in a rectangular patch not four in a square patch), and in Hopkin (2007) it keys down to *Isotoma* spp. It cannot be keyed out completely here because it lacks manubrial teeth, but is easily dismissed as a small dark *Isotoma viridis* Bourlet. The combination of three furcal teeth but no manubrial spines is indicative. To confirm identification the number of setae around the feet needs be counted (9 in *Desoria trispinata*, 11 in *Isotoma* spp).

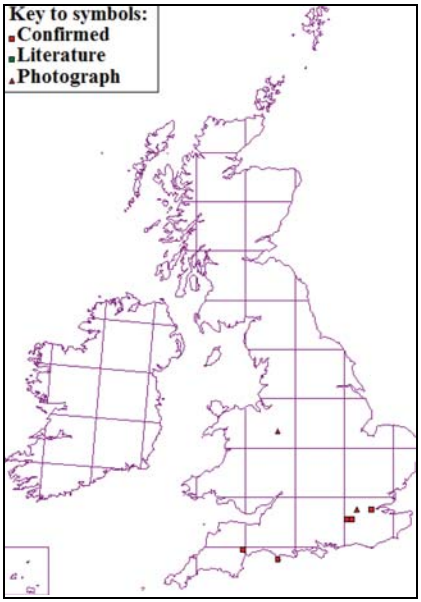

Fig. 6. *Heteromurus major* map.

Roithmeier Burkhardt & Filser (2018) reviewed this species, noting this as a rapidly expanding species capable of dominating soil communities. One of the reasons for its success appears to be its toxicity; wolf spiders fed on this springtail died (Toft & Wise, 1999). The authors suggest it is a good model for an invasive soil organism, and quoted Dorlong (1984) as finding it to have densities upwards of 600,000 animals m^{-2} in Indian forests – a remarkable value for collembolan density,

Fig. 7. *Desoria trispinata*.

over ten times higher than a very rich soil community. It is probable that this extreme value is a mis-calculation or mis-presentation of the data, and that the true value intended by Dorlong was 6410 animals m^{-2}. By way of comparison, the total Collembola population in a UK pine woodland was around 10,000 animals m^{-2} with no species found at densities exceeding 3000 m^{-2} (Shaw & Usher, 1996). Despite this over-statement of its density, *D. trispinata* is undoubtedly a species to watch out for in the UK as it expands its range. Currently it has only been collected in the UK by PJAS, from three urban locations: his garden (near Dorking) 20.ii.2011, the gardens of The University of Roehampton 01.vii.2010, and the gardens of the Natural History Museum in London 02.xii.2015.

Records – all collected by PS: Whitelands College compost heap (Greater London) TQ21943 73603 01.ii.2010; Dorking garden, Surrey TQ17594 47696 20.i.2011; Natural History Museum wildlife garden, South Kensington TQ26546 79015 on 01.iii.2013 and 02.xii.2015.

Folsomia inoculata Stach

This is a blind white species (Fig. 8) in the genus *Folsomia* (diagnosed by abd4-6 being fused) with 2 + 2 stout setae at the distal end of the manubrium (Fig. 9). *Folsomia inoculata* may be spotted by its large, stout head (said to resemble a bulldog), and easily confirmed by the extra-ordinarily large retinacular ridges at the base of the manubrium (Fig. 10), and also heavily sclerotized mouthparts (Fig. 11). *Folsomia inoculata* is described by Hopkin (2007) as rare. In fact *F. inoculata* appears to be widespread and moderately common (Fig. 12), so was either overlooked or has undergone a recent range expansion. It is found in acid leaf litter, both in southern England (including suspended soil, up a tree in old woodland), and was the dominant collembolan in the litter of a cryptogamic garden in Dawyk, Peebles, Scotland

Fig. 8. *Folsomia inoculata*, overall view. Holmwood Common Surrey, 15 July 2012.

(Garside, 2007). This species can be anticipated to occur widely in woodland leaf litter.

Records: Pullwyke Bay, Windermere, Cumbria NY3602, col. "MEB" 05.i.1934; Pen Y Bont, Powys SN570800 col. P. Miles 29.xii.1994; Wimbledon Common TQ233726, col PS 10.vii.1997; Dawyk Gardens, Peebles NT175355, dominant springtail on multiple dates, col Adam Garside 2001–2002; nr Glasgow NS174764, col M McDermott 10.i.2010; Yarner Wood NNR, Devon SX78049 79136, col Matthew Shepherd 13 Dec 2011; Cemmaes, Powys, SH83840 05923, Mid Wales SH85809 11119, col PS 01.iv.2012; Foel, Powys, SH97340 12190 col PS 01.iv.2012; Snowdonia SH90454 12608, col PS 01.iv.2012; Holmwood Common, Surrey TQ17645 47607, col PS 19.vii.2012; Billingsley SO716834, 01.iii.2015 col P. Boardman; Allt nan Uamph stream cave 22.x.2016 col Andy Lewington; Lower Tralligill cave, West Sutherland NC27092090, col 23.x.2016 Andy Lewington.

Poduromorpha

Mesogastrura libyca (Caroli)

This distinctive blue-spotted podurid (Fig. 13) has only been reliably recorded twice before in the UK, both times in Devon. During a sampling expedition for cave

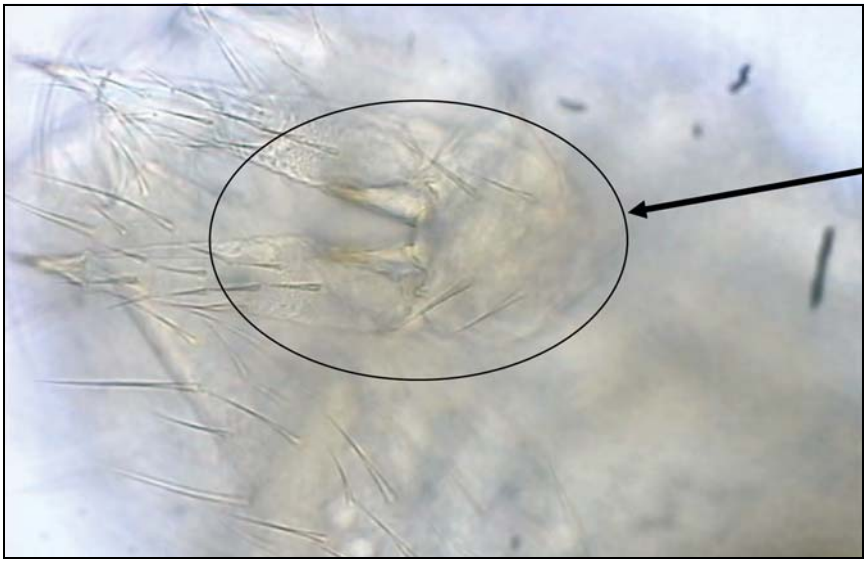

Fig. 9. Ventral surface of manubrium of *Folsomia inoculata*, showing 2 + 2 ventral setae, also part of the ridge structure (see Fig. 11).

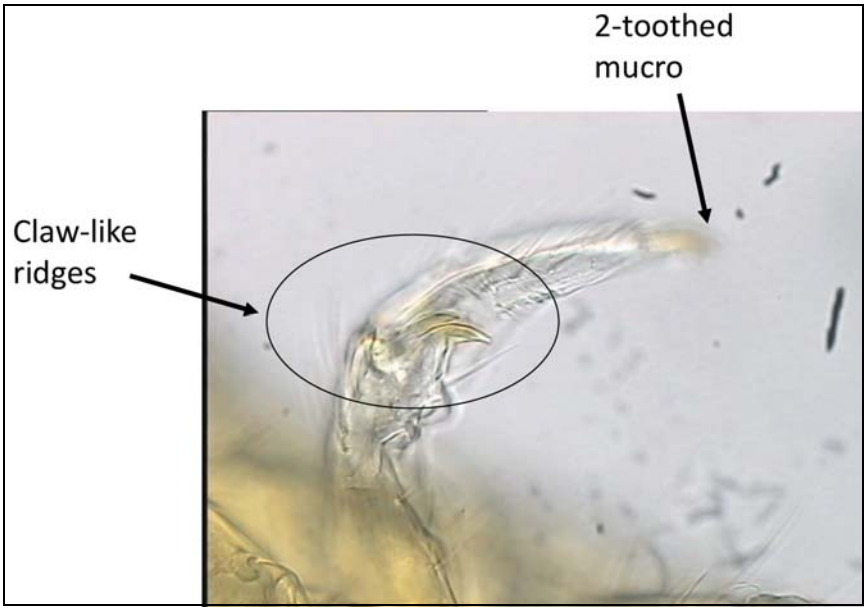

Fig. 10. Furca of *Folsomia inoculata*, showing strange claw-like ridges at manubrial-dental junction.

Collembola 16.xii.2015, soil and leaf litter were collected from the mouth of Rock House Cave (just next to Buckfastleigh quarry), and found to contain many hundreds of a small blue/spotted podurid with a needle like mucro which proved to be this species. It may not be a coincidence that this collection was close to the 1964 record, and in a similar habitat (a cave mouth). This species is known from mainland Europe, but also South America, and has been recorded as a 'troglophile' in a cave system in south-east Australia (Greenslade, 2002). Not fitting with this pattern is a collection of a single animal from the same Lytag site in Tilbury where *Folsomides angularis* was collected.

Records: "on carrots" in Honiton, Devon ST31160060 col. H. Goto 01.viii.1950; in Buckfastleigh quarry, Devon SX74406440 col. 'CM' 26.iv.1964; Rock house quarry SX74306680 Devon col. PS 16.xii.2015; Tilbury power station, Essex, Lytag TQ6561 7648 col PS 03.x.2017.

Marine/Littoral species

Entomobryomorpha

Axelsonia littoralis (Moniez)

This is exclusively a marine / intertidal species, with four old UK records, all from the south coast from the Thames to Cornwall, most UK records being collections made by Richard Bagnall between 1937 and 1938. (one other was found, mis-labelled, on a slide by Frank Turk from Cornwall, 1942). The animal in life is shown in Fig. 14. ST has collected this springtail from seven intertidal sites during wider sampling of coastal micro-arthropods. Compare Fig. 15a with 15b to see the increase in known sites.

Fig. 11. Mouthparts *Folsomia inoculata*, showing strongly sclerotized mandibles.

Records – all collections by ST unless otherwise stated: Canvey Island, Essex TQ78 col R. Bagnall Dec 1937, June 1938, Aug 1938, Nov 1939; Hayling Island, Hants 17.vii.1938, col R. Bagnall; Isle of Grain, Kent TQ8378 col. R. Bagnall 1939; Feock, Cornwall SW82133817 col F. Turk 1942; Rother estuary, Kent 10.ix.1954 col. P. Lawrence; Poole harbour, Hants SZ02516 90735, December 2016; Wyke Regis, Dorset SY64588 76588 10.ix.2017; Falmouth, Cornwall SW81014 31364, 01.x.2018; Looe, Cornwall SX25628 52990, May 2018; Bude, Cornwall SS18059 05924, 29.vii.2017; Castle Cove, Poole harbour SY675776, April 2018; Kimmeridge, Dorset SY90197899, 30.viii.2018; Poole harbour SY99732 91505 March 2018; Poole harbour SY99732 91505, 07.ii.2018; Hannafore point, Looe, Cornwall SX25628 52990 May 2018; Gyllyngvase beach Falmouth, Cornwall SW81014 31364, October 2018.

Mesentotoma dollfusi Salmon

Hopkin (2007) suggested this species was probably widespread but overlooked on southern coasts, but until recently there were only four records. ST has added records from eight new locations, all intertidal and southern (compare Fig. 16a with 16b). We also have a photographic record by Brad Scott from east Sussex (Birling Gap) 20.viii.2017. One notable discovery was a population at Kimmeridge (Dorset) with a distinctive grey colouration, perhaps camouflage against the flaky grey shale which dominates this site (Fig. 17 a,b).

Records – all collections by ST unless otherwise stated: Lundy island SS10400, col. Womersely 1927; Combe Martin, Devon SS580460, col. Womersley 1927; Ilfracombe, Devon SS510470, col. Womersley 1927; Crackington Haven, Cornwall SX140970 September 2001, col. S. Hopkin; Coverack, Cornwall SW768270, col. S. Hopkin; Marazion, Cornwall SW52950-30220, photo by D. Fenwick 29.viii.2013; Chesil beach SY53278627 May 2015, Sep 2017; Sennen, Cornwall SW35136-26170, Dec 2016; Wembury beach, Devon SX51720 48570, Oct. 2016; Lyme Regis, Dorset

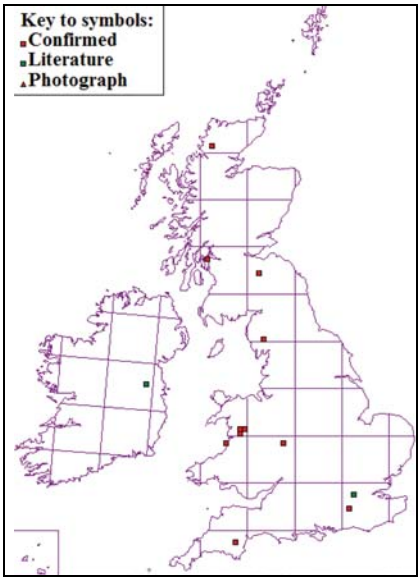

Fig. 12. *Folsomia noculata* distribution map.

SY32789131, Oct 2016; Osmington Mills, Dorset, SY734820 Sep 2016; Ringstead Bay, Dorset SY761813 June 2016, Aug 2016, Jan 2017; Pondfields, Dorset SY87306 79557 Nov 2016; Kimmeridge, Dorset SY90197899; Swanage, Dorset SZ03950 78709 Sep 2016, Oct 2016; Looe, Cornwall, SX23275148 28.ii.17; Lee Bay, Devon SS48074678, 24.ix.2017; Rhossili beach, Gower SS37106 91615, 30.iv.2017; Birling Gap Kent (sea cliff) 06.viii.2017, photo by B. Scott.

Poduromorpha

Friesea acuminata (Denis)

Friesea is a genus of predatory podurids which mainly live in leaf litter, characterised by having three or more short stout anal spines at the end of a short rounded abdomen. *Friesea acuminata* is unusual in living inter-tidally, and having six long thin anal spines at the end of a rather pointed abdomen (acuminata means 'pointed'). It is also grey/yellow, unlike other *Friesea* species which are universally pale grey (Fig. 18). Until recently, all UK records were between 1918 and 1938, collected by Richard Bagnall. In 2016 this springtail turned up in inter-tidal collections from two locations in Dorset (Kimmeridge and Pondfields) with a third collection in 2018 at nearby Worbarrow. These are the dense cluster of points in on the south coast of its distribution map (Fig. 19). It is all but certain that this species is widespread but overlooked, since few entomologists search under the inter-tidal boulders where it seems to live.

Fig. 13. *Mesogastrura libyca*

Fig. 14. *Axelsonia littoralis* in life, along with the marine prostigmatid mite *Halotydeus hydrodromus*.

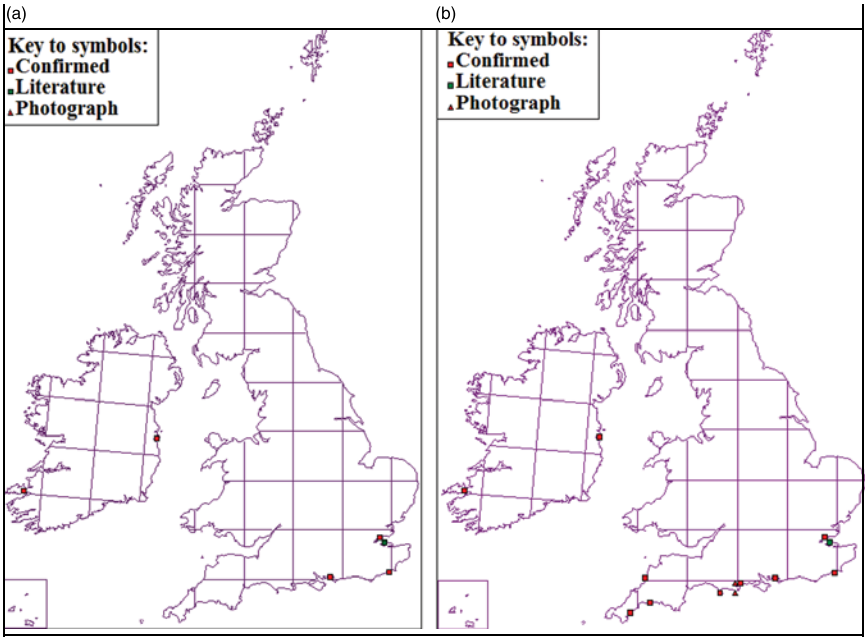

Fig. 15. *Axelsonia* maps. (a) *Axelsonia littoralis* map pre-Steve Trewella. (b) *Axelsonia littoralis* map 2018.

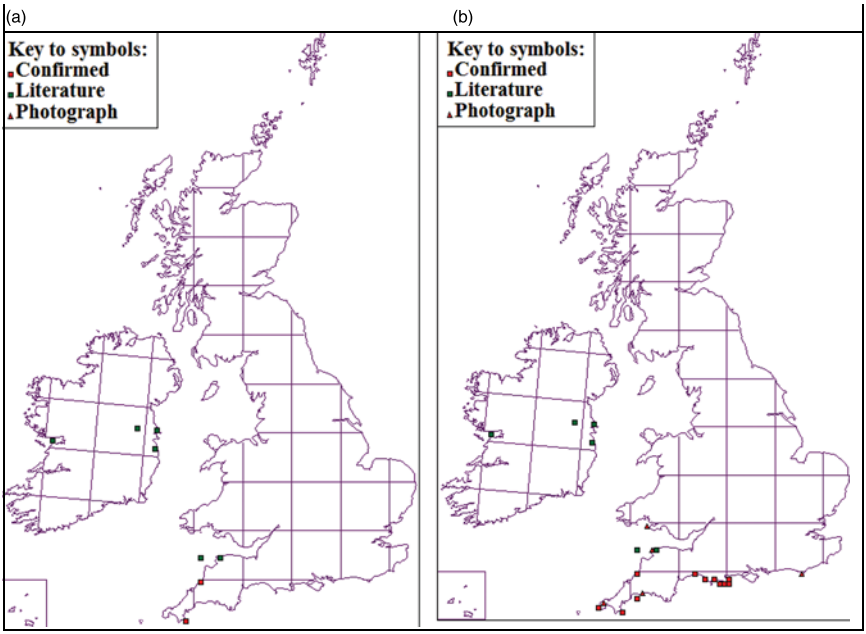

Fig. 16. *Mesentotoma* maps. (a) *Mesentotoma dollfusi* pre-Steve Trewella. (b) *Mesentotoma dollfusi* 2018.

Records – all collections by ST unless otherwise stated:

Swanage, Dorset SZ0279, col. R. Bagnall 1918; Canvey Island, Hants TQ7782, August 1937, Aug 1938, col R. Bagnall; Hayling Island 17.vii.1938, col R. Bagnall; Porthcawl, Glamorgan SS820770 08.iv.1938 col. R. Bagnall; Pondfields, Dorset SY87306 79557 Nov 2016; Worbarrow, Dorset SY86973 79928, March 2018; Kimmeridge, Dorset SY9019 7899, Sep 2016, Nov 2016.

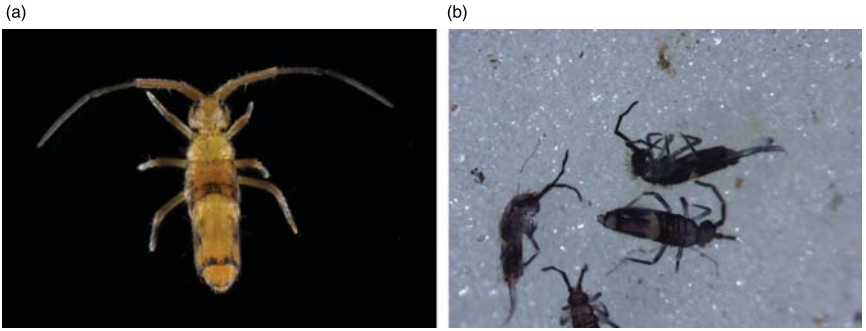

Fig. 17. *Mesentotoma dollfusi*. (a) *Mesentotoma dollfusi* normal colour scheme; Pondfields, Dorset, September 2016. (b) *Mesentotoma dollfusi* from Kimmeridge, Dorset, October 2016, showing grey colour form.

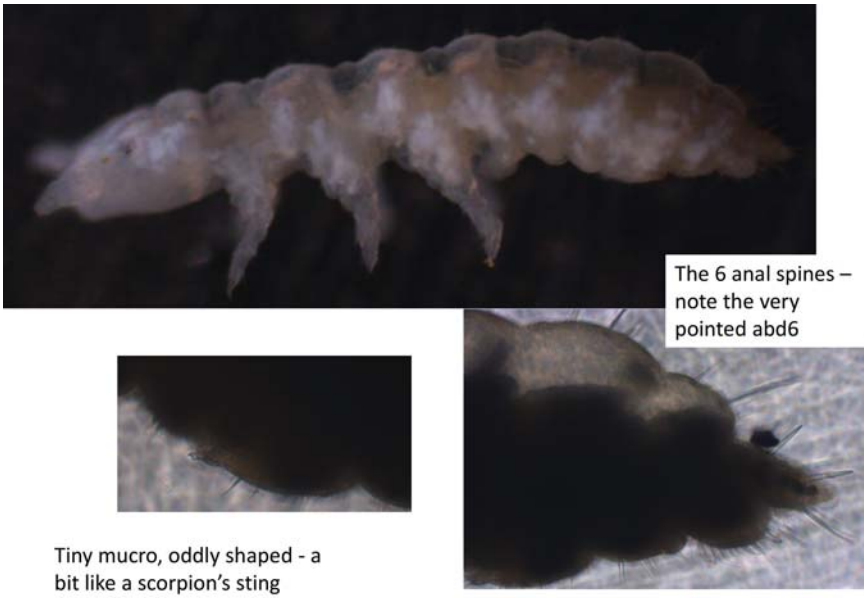

Fig. 18. *Friesea acuminata* (Denis 1925), from under an inter-tidal boulder, Kimmeridge, Dorset, September 2016. Collected by Steve Trewella.

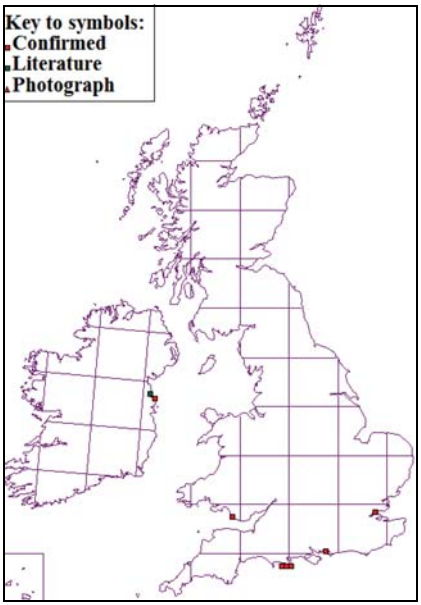

Fig. 19. *Friesea acuminata* map.

Megaphorura sp

Steve Trewhella collected an onychiurid from the strand line at Chesil Fleet, Dorset in November 2016 SY53278627 and again May 2017, which (using Hopkin, 2007) keyed to *Megaphorura arctica* (Tullberg). This is (as its name suggests) an arctic species, but apparently this same species was recorded from a sea cave on Skomer island in July 1977 (Pitkin, 1979). A typical onychiurid (Fig. 20), white and blind with two anal spines, to establish identification these animals need to be cleared in lactic acid/glycerol to check the distribution of pseudocelli and for the presence/absence of a remnant furcal fold. The key steps in Hopkin (2007) include having no furcal remnant (most such onychiurids have a tiny fold like a capital letter D on abd 4) and no pseudocelli on thorax 1. These were also keyed using Pomorski (1998), which showed it to be in the Thalassaphoruridae, but not in the genus *Thalassaphorura*. Given that

Fig. 20. *Megaphorura arctica* in life, Fleet, May 2016.

M. arctica is a large yellowish species of arctic tundra, while the UK specimens are small-medium sized, pale animals of the littoral zone, and that the pseudocelli do not match the pattern for *M. arctica* it is likely that these are some other (potentially undescribed) species. Further investigations are underway.

Discussion

The list above includes one proven invasive (*Desoria trispinata*), plus two more likely non-natives (*Entomobrya* nr *imitabilis* and *Mesogastrura libyca*). The status of *Heteromurus major* remains unclear; it is a strongly southern species, first found in the UK in 2000 (suggesting a recent arrival), but it is native European species which has been found in rural UK ancient woodland (Bookham Common)s, suggesting it is of long standing.

The other Collembola described above must be presumed to be native. *Entomobrya intermedia* is considered a UK endemic (Jordana 2012), and now that it is shown to be genetically distinct from *E. nivalis* and readily separated visually from it, this species deserves to be more widely known and should certainly be included in any updated key to UK Collembola. It seems to have a strong southern bias, being largely absent from Scotland. Another species that seems to have been widely overlooked is *Folsomia inoculata*, likely found in leaf litter of old woodlands on acid soil around the country.

The first three coastal springtails (*Axelsonia littoralis, Friesea acuminata, Mesentotoma dollfusi*) are examples of native species being overlooked because they occupy unfamiliar habitats. They were collected by Richard Bagnall from inter-tidal habitats in the 1930s, and hardly (if at all) since, presumably because Collembola collectors avoid inter-tidal zones, while rock pool researchers do not look for Collembola. They seem to have a southerly distribution (Figs 15, 17, 18) but this may be an artefact of limited sampling. The fourth, a *Megaphorura* sp., may be an overlooked new taxon, but needs to be included as part of a wider molecular survey of the UK's Onychiuridae.

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References

Bowden, J., Haines, I. & Mercer, D. 1976. Climbing Collembola. *Pedobiologia* **16:** 298–312.

Bretfeld, G. 1999. Synopses on Palaearctic Collembola Vol. 2: Symphypleona. *Abhandlungen und Berichte des Naturkundemuseums Görlitz* **71**: 1–320.

Dorlong, V. T. 1984. *Ecological Studies of Soil Arthropods in Forest and Jhum Systems of Laitkor, Meghalaya*. Thesis. North-Eastern Hill University.

Faria, C. M. A. 2015. *Colonisation and diversification in invertebrates: looking within species on islands to connect pattern and process*. PhD thesis: University of East Anglia.

Faria, C. M. A., Shaw, P. & Emerson, B. C. (under review) Evidence supporting the northern European Pleistocene persistence of UK Collembola. *Journal of Biogeography*.

Fjellberg, A. 2007. The Collembola of Fennoscandia and Denmark, Part II: Entomobryomorpha and Symphypleona. *Fauna Entomologica Scandinavica* **42.**

Garside, A. 2007. *The microarthropods of Dawyck Cryptogamic gardens*. M. Phil thesis, Dundee Abertaye University.

Greenslade, P. 2002. Systematic composition and distribution of Australian cave collembolan faunas with notes on exotic taxa. *Helictite* **38**: 11–15.

Hopkin, S. P. 1997. *Biology of the springtails*. Oxford University Press.

Hopkin, S. P. 2007. *A Key to the Collembola (Springtails) of Britain and Ireland*. FSC Publications.

Jordana, R. 2012. Synopses on Palaearctic Collembola Vol. 7/1: Capbryinae & Entomobryini. – *Soil Organisms* **84**: 1–391.

Leinass, H. P. 1983. Winter strategy of surface-dwelling Collembola. *Pedobiologia* **25:** 235–240.

Lubbock, J. 1873. *Monograph of the Collembola and Thysanura*. Ray Society, London.

Lukic, M., Delic, T., Zagmajster, M. & Deharveng, L. 2018. Setting a morphological framework for the genus *Verhoeffiella* (Collembola, Entomobryidae) for describing new

troglomorphic species from the Dinaric karst (Western Balkans). *Invertebrate Systematics* **32**: 1118–1170.

Mari Mutt, J. 1980. A review of *Heteromurus* s. str. (Insecta: Collembola: Entomobryidae). *Transactions Illinois State Academy of Sciences* **72**: 29–50.

Pitkin, B. R. 1979. *Onychiurus arcticus* (Tullberg) (Collembola: Onychiuridae) an interesting new record to Britain, with a note on variation and distribution. *Revue d'Ecologie Et De Biologie Du Sol* **16**: 449–452.

Pomorski, R. J. 1998. *Onychiurinae of Poland (Collembola: Onychiuridae)*. Wroclaw, Poland: Polish taxonomical society.

Roithmeier, O., Burkhardt, U. & E. Filser, J. 2018. *Desoria trispinata* (MacGillivray, 1896), a promising model Collembola species to study biological invasions in soil communities. *Pedobiologia* **67**: 45–56.

Shaw, P. J. A. 2013. The use of inert pads to study the Collembola of suspended soils. *Soil Organisms*. **85**: 69–74.

Shaw, P. J. A. 2015. How high do Collembola climb? Studies of vertical migration in arboreal Collembola. *Soil Organisms* **87**: 227–235.

Shaw, P. J. A. & Benefer, C. 2015. Development of a barcoding database for the UK Collembola: early results. *Soil Organisms* **87**: 197–202.

Toft, S. & Wise, D. H. 1999. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different qualities. *Oecologia* **119**: 191–197.